

# Kinematic analysis of maiden flight of Odonata

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**Key words:** Odonata, dragonfly, maiden flight, slow motion analysis, wing beat frequency, flight speed.

## ABSTRACT

The maiden flight of five species of Odonata of different families was filmed by slow motion up to 500 f/s and analysed frame by frame. The aim of this study was to find out if the maiden flight differs among various species as well as between teneral and adults within the same species with respect to wing beat frequency, phase-relationship between fore- and hind wings, flight speed and acceleration. All the values of the flight parameters were much lower in maiden flight than in the flight of adults. The possible reasons for the weakness of the maiden flight are discussed.

## INTRODUCTION

The maiden flight is an important phase in the life of an insect. It ensures survival and is the first step for the distribution of the adults (Conrad & Hermann 1990). Odonata are captured mostly when they are not in flight, e.g., during oviposition or while roosting at low temperatures (Hilfert-Rüppell 2004; Rüppell et al. 2005). Emergence and the following hardening of the body and wings represent a delicate phase during their life history (Corbet 2004; Wildermuth 2008). Large species such as *Anax imperator* Leach emerge at night and start their first flight at dawn. This flight in semidarkness can be considered as protection against bird predation at the time of emergence (Corbet et al. 1960; Corbet 1962). Individuals that emerge and start to their first flight in daytime are prone to predation by birds (Kennedy 1950; Corbet 1962; Rudolph 1985). In a study on the nestlings' food of the Savi's warbler (*Locustella luscionides*) Tschan (1995) found that 94% of the captured Odonata were larvae ready for emergence or teneral imagines. During maiden flight the wings are not yet stiff and the flight appears slow and clumsy (Corbet et al. 1960).

Supply and development of the flight muscles (Marden 2000) may play a major role during the maiden flight. Leaving these aspects aside we will focus on the kinematics and on the analysis of the flights, comparing the maiden flight with adult flight.

Flight movements of all insects can be explained by the wing movements. (Grodnitzky 1999; Nachtigall 2003). Odonata beat the two pairs of wings independently from each other in most cases. The flight parameters wing beat frequency, phase relationship of fore wings and hind wings, ratio of duration of up- and down-stroke, flight speed and acceleration vary a lot. Anisoptera usually fly faster and longer than Zygoptera, but the latter show better manoeuvrability and acceleration, which is highest in Calopterygidae (Rüppell 1989, 2005, 2009).

The flight muscles are in action for the first time during the maiden flight, as is the whole sensory and motor flight system. To compare the teneral flight with that of adults we measured the wing beat frequencies and the variations of the flight velocities. The wing beat frequency generates the airflow and vortices and thereby largely determines flight speed, acceleration and flight manoeuvres (Rüppell 1989; Rüppell et al. 2005). We expected that wing beat frequencies and the flight speeds of tenerals were lower than those of adults, what would invite discussion.

## MATERIALS AND METHODS

By means of a photographic camera capable of slow motion filming (Casio EX F1) the first flights of different Odonata species were filmed in the summers 2009 and 2010. The filming frequencies were 250 and 500 frames per second (f/s). We analysed five species of different sizes and from the suborders Zygoptera and Anisoptera.

Flight parameters are influenced by body parameters, so the latter are important for comparison (Table 1). The values for *Coenagrion puella* (Linnaeus) are interpolated from other species of similar size as *Ischnura elegans* (Vander Linden) and *Platynemesis pennipes* (Pallas) (Grabow & Rüppell 1995).

At a garden pond 15 km east of Braunschweig (52°26'N, 10°23'E) we waited for freshly emerged individuals and took film shots when they took off. Adults were filmed between 9:00 - 14:00 h local time. Here we observed *Cordulia aenea* (Linnaeus) (8 adult and 16 maiden flights), *Aeshna cyanea* (O.F. Müller) (13 adult and one maiden flight) and *C. puella* (2 maiden flights). *Calopteryx splendens* (Harris) (> 10 adult and 8 teneral flights) was filmed at the river Oker 20 km north of Braunschweig, when we walked along the bank side and the teneral odonates then took off. The term "teneral" is used according to Corbet (2004) for only freshly emerged individuals that were not hardened yet and were perching near to their exuvia and had shining wings when flying. We applied this method also for *Libellula quadrimaculata* Linnaeus (3 adult and 2 maiden flights) and *C. puella* (3 adult

Table 1. Body parameters of the investigated species. Body length [mm] after Dijkstra & Lewington 2006; Fw length [mm] after d'Aguilar & Dommanget 1998; weight [g] and wing load [ $\text{mg} \cdot \text{cm}^{-2}$ ] after Grabow & Rüppell 1995. The 'ca' values for *C. puella* are interpolated.

Species and sex	Body length	Fw length	Weight	Wing load
<i>Calopteryx splendens</i> ♂	45-48	27-32	120	13.7
<i>Coenagrion puella</i> , sex unknown	33-35	♂ 15-22 ♀ 18-24	ca 30	ca 14
<i>Aeshna cyanea</i> ♂	67-76	44-52	729	39.0
<i>Cordulia aenea</i> ♂	47-55	29-34	375	35.2
<i>Libellula quadrimaculata</i> ♂	40-48	32-36	382	30.6

and 6 teneral flights) at a forest pond 10 km north-east of Braunschweig. The suitable films were analysed with the aid of the computer program "Quick Time" version 7.55, which offers frame by frame viewing. Gliding phases of the adult flights were excluded from calculations of the wing beat frequencies. As successful maiden flights are directed upwards in the beginning, the upward velocities were measured. These were measured by marking the shift of the individual's image on a movable foil placed on the screen of the computer (Toshiba Satellite P 100). When the camera was moved, prominent structures of the background were drawn on the foil and were covered by these structures on the film when measuring the dragonfly's body displacement. These velocities were some mm to cm per time intervals of 0.04 s and were calculated to 1 s. The lengths of the bodies were taken as median value from Dijkstra & Lewington (2006) and the lengths of the fore wings as median value from d'Aguilar & Dommanget (1998). All measured distances were corrected by a factor derived from the comparison of the values from the literature with the lengths measured on the screen. Only those cases with the flight path perpendicular to the direction of filming were used for the analysis.

The upward flight path in both maiden and adult flight was never exactly vertical. Nevertheless, we use the term 'vertical flight velocity' even when horizontal movements were also included.

To analyse wing beat frequencies, velocities and accelerations we used Excel and SPSS 17.0 (Mann-Whitney-*U*-test). The durations of up stroke and down stroke (up:down ratio) which are together one wing beat period and the phase shifting of hind- and fore wings were calculated by counting the numbers of film frames. A phase shifting of 100% means beating the two pairs of wings counterstrokingly, 50% signifies beating them with a delay of half of the duration of the down or upstroke and 0% means beating them in parallel. All filming was conducted on sunny days at ambient temperature between 22°C and 26°C.

## RESULTS

### Preflight wing beating

Before take off the teneral individuals of *Cordulia aenea* wing whirled for some seconds with a frequency of 27-30 Hz. Afterwards they beat their wings while still clinging to the perch. In *C. aenea* we counted 2-50 wing beats (mean 14.3, s.d. 13.3,  $n = 10$ ) before take off. The stroke frequency then was low, in *Aeshna cyanea* 16.5 Hz ( $n = 6$ ) and in *C. aenea* 17.7 ( $n = 26$ ). In *C. aenea* this stroking was performed mostly by the fore wings, which had a wider stroke amplitude (nearly 90°) than the hind wings and were beaten in a few cases nearly to the point touching each other in backward position. The hind wings were hold nearly still in much of this preparation for take-off. Because of the different filming-method no preflight wing beating of the other species could be recorded.

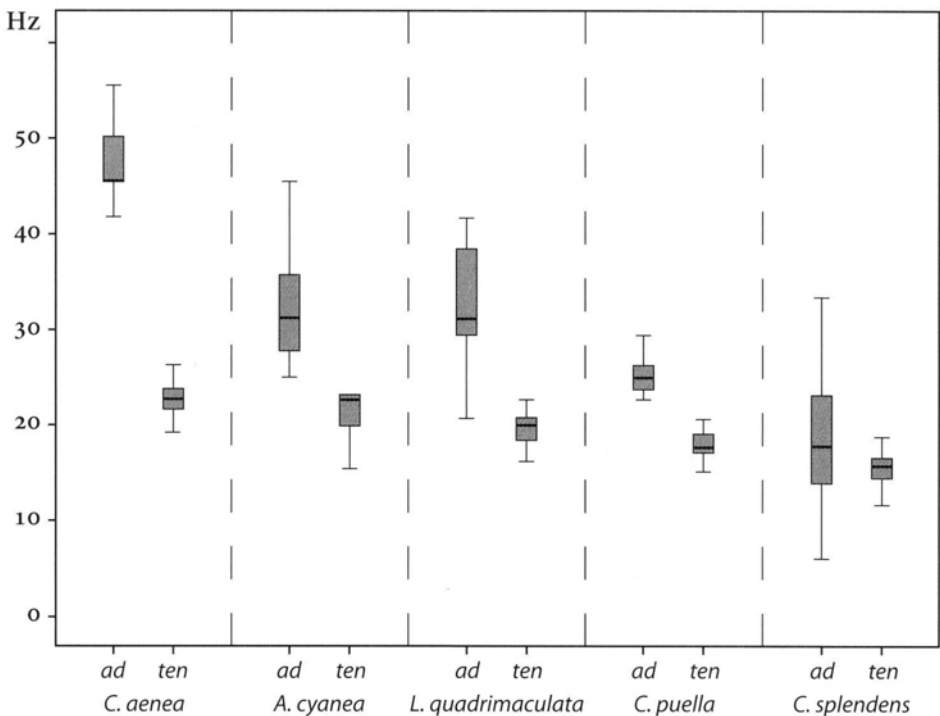


Figure 1: Wing beat frequencies (Hz) of adults (ad) and teneral (ten). Boxplots showing the median (thick line), 50% of the values (box) as well as range (vertical lines). Sample sizes correspond to those of Table 2.

## Wing beat frequencies

In all species the wing beat frequencies of the first flights of freshly emerged individuals were significantly lower than those of the adults (Mann-Whitney-*U*-test: *Calopteryx splendens*:  $U = 3,511$ ,  $p = 0.00$ ; *Coenagrion puella*:  $U = 40$ ;  $p = 0.00$  *A. cyanea*:  $U = 31$ ;  $p = 0.00$  *C. aenea*:  $U = 254$ ;  $p = 0.00$  *Libellula quadrimaculata*:  $U = 4$ ;  $p = 0.00$ , Fig. 1, Table 2).

The wing beat frequencies of the adults varied more than that of the teneral, shown by the standard deviations. This is not only true within one species but also when we compare all teneral with all adults. The smallest differences in the mean value of wing beat frequencies occurred in *C. splendens*, which had the lowest frequencies in both stages. The largest differences were found in *C. aenea* which showed the highest frequencies in the adult stage.

## Phase shifts

The beginning of a new wing beat was led by the hind wings in Anisoptera and by the fore wings in Zygoptera. In Anisoptera the variability of the degree of phase shifting was larger in adults than in teneral. Adult *A. cyanea* and *C. aenea* beat both wing pairs sometimes parallel but more frequently by counterstrokes and mostly phase shifted. The hind wings then began a stroke of about 30-40% of the duration of the down stroke earlier than the fore wings. Teneral mostly beat both wing pairs phase shifted, but in one case a teneral *C. aenea* taking off for maiden flight in backward direction moved its wings in parallel for nine strokes. Exact

Table 2. Wing beat frequencies (F) of teneral (ten) and adult (ad) individuals of all species; and percentage of mean teneral wing beat frequency [adult = 100%]. The number of wing beats are the numbers recorded on film; given are the highest value (max) and mean  $\pm$  s.d.

Species and sex	F ten			F ad			% F	# flights		# wing beats	
	max	mean	s.d.	max	mean	s.d.		ten	ad	ten	ad
<i>Calopteryx splendens</i> ♂	18.8	15.4	2.1	30.0	18.6	5.7	82.8	5	5	59	167
<i>Coenagrion puella</i> , sex in ten unknown	25.0	18.2	1.6	33.3	25.5	2.6	71.4	4	1 ♂	74	26
<i>Aeshna cyanea</i> ♂	23.2	22.0	3.2	50.0	32.4	5.2	67.9	1	4	15	91
<i>Cordulia aenea</i> ♂	27.7	22.5	2.0	55.6	47.6	5.5	47.3	5	5	125	103
<i>Libellula quadrimaculata</i> ♂	25.0	20.1	2.1	41.7	33.2	6.2	60.5	2	3	13	15

counterstroking did not occur in maiden flight of *C. aenea* with one recorded exception of two wing beats, the delay of the fore wings being nearly 100%.

In teneral individuals of *C. puella* as well as in most adult males in tandem position, fore- and hind wings nearly counterstroked. But phase-shifting was also observed: in one adult male the fore wings began a stroke 42.3% - 46.7% earlier of the duration of the downstroke than the hind wings and in some teneral individuals this was 30-43%. When tenerals flew backward this phase shifting was smaller and made up only 8-10% at the moment of backward-acceleration. This beating of the two pairs of wings was done mostly in parallel. When pursued at a distance of about half a meter by one of the filming authors three teneral *C. puella* showed a sudden parallel wing beat forward at high angles of attack which changed the direction of flight extremely. In *C. splendens* both, adults and tenerals, beat their wing pairs nearly in parallel, only the hind wings sometimes had some delay of ca 5%. Only the courting flight in *C. splendens* was counterstrokingly.

### Ratio upstroke:downstroke

The ratio upstroke:downstroke did not differ between maiden and adult flights. This ratio was in Anisoptera ca 1:1. The upward stroke sometimes was 5-10% longer. In *Zygoptera* the upstroke was shorter than the downstroke, nearly 0.7:1. In *C. puella* this ratio in two recorded maiden flights was nearly 1:1, in *C. splendens* 0.73:1, but 1:1 when wing stroke pauses in backward position were included.

### Velocity of upward flights

We could not measure the velocity of upward flights in *Zygoptera* during maiden flights, because they were directed more or less horizontally. The flight velocity during upward flights of Anisoptera was definitely lower in maiden flights than in the flights of adults (Fig. 2). Tenerals flew at maximum speed of 50-80 cm/s, whereas adults were twice as fast when flying fast. When starting the maiden flight the teneral of *A. cyanea* was hampered by dense vegetation that served as emergence substrate. Hence, it first had to reach free flight space before it was able to accelerate. While the speed of all maiden flights when reaching it's maximum varied little, it varied more in adult flights from flying on the spot to the flight velocities presented here. Tenerals never could be seen flying on the spot. Similar differences we found in the vertical accelerations, which are the slopes of the flight velocities (Fig. 2). These accelerations of the maiden flights were constantly lower than the corresponding ones of the adult flights.

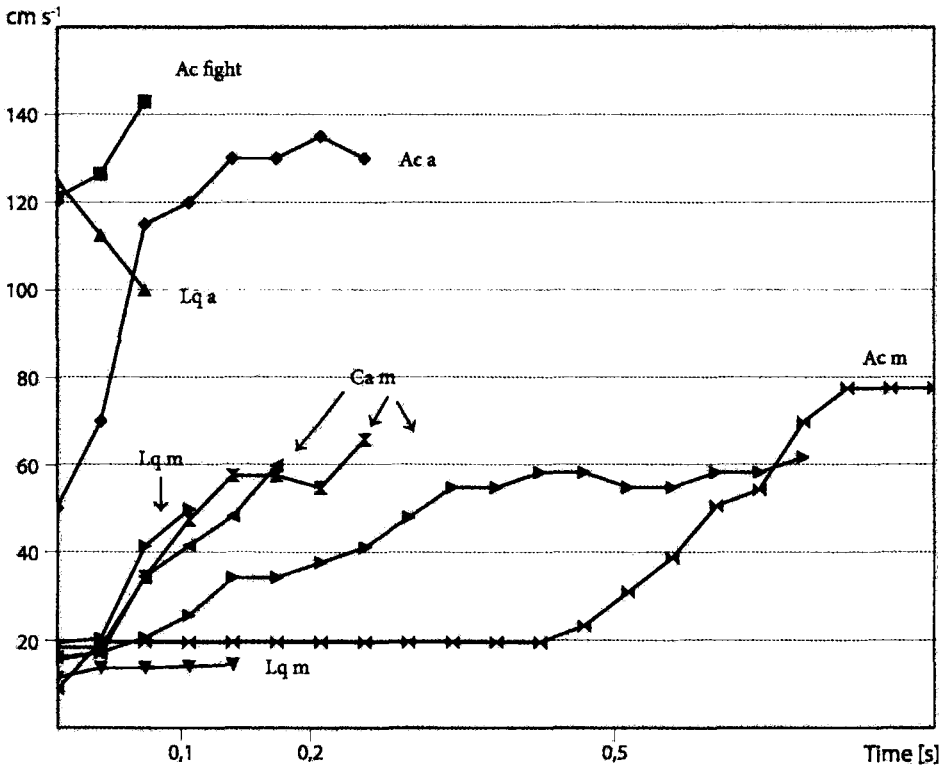


Figure 2: Velocities during upward flight (only the vertical component) of teneral (measured from take-off on) and adult odonate species. Ac ad: *Aeshna cyanea* adult, flying upward after floating on the water; Ac fight: *A. cyanea* flying upward during fight with rival; Lq a: *Libellula quadrimaculata* adult, flying upward after a frog's attack; Ac m: *A. cyanea* maiden flight; Lq m: *L. quadrimaculata* maiden flight; Ca m: *Cordulia aenea* maiden flight (three examples).

## DISCUSSION

Corbet (1960) described the maiden flight of *Anax imperator*. He recognized the softness of the bodies, the increase of the wing beat frequency before take-off and how slow these first flights were: "Some were still so soft that the abdomen hung downwards from its own weight." and "...the only sound to be heard was made by the fluttering wings of those unfortunates that had collided with branches and fallen into the water." *A. imperator* is a large dragonfly and emerges during the night as do many large species (Corbet 1962; Trottier 1973). The maiden flight at dawn occurs at great numbers and within a short time offering social shelter for

the individuals. The warming up is done by wing whirring for more than 20 minutes (Corbet 1960).

During daytime, especially when the temperatures are high, warming up is easier and can be shorter. The maiden flight should be stronger and faster. During sunshine we saw only short wing whirring and only a few preflight wing beats in *Cordulia aenea*. Probably these first wing beats after emergence serve not only for warming up but also for spreading the muscles and adjusting the wing joints. Because the wings touch each other sometimes in backward position the wing beat angles of teneral exceed those of adult flights, the latter encompassing 70-90° (Rüppell 1989), by 30-40°.

During emergence and maiden flight Odonata are especially prone to predation by birds (Kennedy 1950; Corbet 1962; Rudolph 1985). At our pond regular predation flights of sparrows (*Passer domesticus* and *P. montanus*) and blackbirds (*Turdus merula*) are seen at times when Odonata emerge, the birds feeding their nestlings with odonates. Teneral individuals hardening or preparing for flight were easily captured by the birds hovering in the vegetation. But once the dragonflies had started their maiden flight several individuals were able to escape. The velocities of teneral odonates in upward flight, at 50-80 cm·s<sup>-1</sup>, are much lower than those of songbirds such as sparrows and blackbirds in forwards flight (Mc Laughlin & Montgomerie 1990; Evans & Drickamer 1994). Yet, the speed when flying upwards from hovering must be much lower in these bird species, too, because they cannot take speed in the open air to fly fast upwards like e.g. bee-eaters (*Merops* spp.). Furthermore the exact time of take-off of the maiden flight is unpredictable, reducing the chance of discovery. Thus, the chance to escape bird predation can be considerable for dragonflies performing their first flight even during the day. The flight of Zygoptera is much weaker than that of Anisoptera, as indicated by their wing beat frequencies and their flight speed in general (Rüppell 1989; Rüppell & Hilfert-Rüppell 2009). This assumption is supported by the small differences in the wing beat frequencies in adult and teneral individuals of *Calopteryx splendens* and *Coenagrion puella*. The wing beat frequency of adults surpassed those of teneral in maiden flight for only about 17.2%, whereas in the anisopteran *C. aenea* (Fig. 3) the difference was 51.8%.

The velocity of the maiden flight of Anisoptera can be compared with that of adult *Epiophlebia superstes* (Selys) (Anisozygoptera), the poorest flyer among Odonata, with high wing loading and primitive wing-joint kinematics (Pfau 1986). In a recorded case an adult male of this ancient species took off only after a long time of wing whirring and 22 full wing beats before it became airborne. Then it took another 0.06 s before any forward speed was achieved and the acceleration was low (Rüppell & Hilfert 1993). Yet this poor flyer when airborne was faster in vertical flight than all the investigated Anisoptera during maiden flight in this study. Probably because of their weakness the maiden flights of *C. puella* were directed only at the beginning a little upward but after that more or less horizontally. Astonishingly





Figure 3: *Cordulia aenea* starting its maiden flight, 9 May 2006. Photo by GR.

these weak flyers were shortly able to perform parallel wing beats forward with high angles of attack, changing flight direction significantly. This might be an innate behaviour to escape predators. Furthermore it is the shortness of their maiden flight (only some metres), their small size and inconspicuousness that save them to some extent from being captured. Simultaneous mass maiden flights may be another way to minimize losses by predation. In *Zygoptera* we saw mass maiden flights in *C. puella* with hundreds of individuals taking off suddenly, then there was a break of ca 10-15 min, followed by another mass maiden flight (unpubl.).

Some maiden flights that we observed failed and the individuals plunged into the water. It is concluded that the teneral have to wait with the start until they are physiologically ready. On the other hand they must leave the emergence site as soon as possible in order to prevent predation. Maiden flights must be a trade-off between a safe take-off as fast as possible after emergence and flying safely away from the water. The small fluctuation in wing beat frequency and phase shifting suggest that both flight parameters are used within their optimal ranges in maiden flight, and therefore that these individuals are operating near the limit of flight. Wang & Russell (2007) and Usherwood & Lehmann (2008) found a similar phase-shifting in the flight of adult *Anisoptera* to be aerodynamically very effective. The wing beat frequencies and the phase shifting of both wing pairs as we found in maiden flights must be the most economic way to produce lift and thrust at this stage to move the teneral away from water. If the first take off failed the power of the teneral seemed to be reduced very much, so it took in some cases several hours before a new attempt.

The low wing beat frequencies and low flight speeds are probably due to the soft wings of the freshly emerged individuals. Another reason for the weak flight of teneral should be the low power output of their flight muscles, which increase together with the muscle mass during maturity (Marden 1989). The neural coordination of the flight system seems to work already, controlling the up : down stroke ratio and the different ratios of phase shifting between fore wings and hind wings. Phase shifting with ca 30% delay of the fore wings is used in the vast majority in *Anisoptera* during maiden flight but nearly counterstroking and parallel stroking did also occur, although being very rare. In *Zygoptera* (excluding *Calopterygidae*) counterstroking occurred both in teneral and adults as well as phase-shifted wing beating. Short parallel stroking in teneral when fleeing and in adults when accelerating backward (unpubl.) was found in *Zygoptera*, too. Thus the major flight coordination patterns of *Anisoptera* and *Zygoptera* (Rüppell 1989) already exist.

The power input of the flight muscles probably distorts the soft wings more than the hardened wings of adults, especially during acceleration of wings for take-off. In order to prevent crash during maiden flight this power has to be adjusted accordingly. This matches our observation that all recorded maiden flights exhibited low wing beat frequencies between 15-22 Hz. Only in dry and hardened condition the wings of odonates are able to display the full economic efficiency (Woot-

ton 1991) of their sophisticated ultra-structural elements (Gorb 1999; Song et al. 2007) enhancing elasticity and stability.

## ACKNOWLEDGEMENTS

Thanks to Jan Pascal Rüppell for assistance in the field. Hansruedi Wildermuth improved the manuscript and Andrea Worthington and Michael May gave helpful remarks.

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